

## University of Groningen

### **A new European testate amoebae transfer function for palaeohydrological reconstruction on ombrotrophic peatlands**

Charman, Dan J.; Blundell, Antony; Alm, Jukka; Bartlett, Sue; Begeot, Carole; Blaauw, Maarten; Chambers, Frank; Daniell, John; Evershed, Richard; Hunt, John

*Published in:*  
Journal of Quaternary Science

*DOI:*  
[10.1002/jqs.1026](https://doi.org/10.1002/jqs.1026)

**IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.**

*Document Version*  
Publisher's PDF, also known as Version of record

*Publication date:*  
2007

[Link to publication in University of Groningen/UMCG research database](#)

*Citation for published version (APA):*

Charman, D. J., Blundell, A., Alm, J., Bartlett, S., Begeot, C., Blaauw, M., Chambers, F., Daniell, J., Evershed, R., Hunt, J., Karofeld, E., Korhola, A., Kuester, H., Laine, J., Magny, M., Mauquoy, D., McClymont, E., Mitchell, F., Oksanen, P., ... Yeloff, D. (2007). A new European testate amoebae transfer function for palaeohydrological reconstruction on ombrotrophic peatlands. *Journal of Quaternary Science*, 22(3), 209-221. <https://doi.org/10.1002/jqs.1026>

#### **Copyright**

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

#### **Take-down policy**

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

# A new European testate amoebae transfer function for palaeohydrological reconstruction on ombrotrophic peatlands

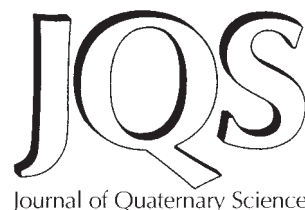
DAN J. CHARMAN,\* ANTONY BLUNDELL and ACCROTELM MEMBERS†

School of Geography, University of Plymouth, Plymouth, UK

Charman, D. J., Blundell, A. and ACCROTELM members. 2006. A new European testate amoebae transfer function for palaeohydrological reconstruction on ombrotrophic peatlands. *J. Quaternary Sci.*, Vol. 22 pp. 209–221. ISSN 0267–8179.

Received 8 December 2005; Revised 13 February 2006; Accepted 15 March 2006

**ABSTRACT:** Proxy climate data can be obtained from reconstructions of hydrological changes on ombrotrophic (rain-fed) peatlands using biological indicators, such as testate amoebae. Reconstructions are based on transfer functions, relating modern assemblage composition to water table and moisture content, applied to fossil sequences. Existing transfer functions in Europe and elsewhere are limited geographically and there are often problems with missing or poor analogues. This paper presents a new palaeohydrological transfer function based on sampling raised mires from across Europe. Relationships between assemblages and hydrological variables are described using ordination analyses. Transfer functions are developed for depth to water table ( $n = 119$ ) and moisture content ( $n = 132$ ) with root mean squared errors (RMSEP) of 5.6 cm and 2.7% respectively. Both transfer functions have an  $r^2$  of 0.71, based on 'leave one out' cross-validation. Comparisons with an existing transfer function for Britain show that the European transfer function performs well in inferring measured water tables in Britain but that the British data cannot be used to infer water tables for other European sites with confidence. Several of the key missing and poor analogue taxa problems encountered in previous transfer functions are solved. The new transfer function will be an important tool in developing peat-based palaeoclimatic reconstructions for European sites. Copyright © 2006 John Wiley & Sons, Ltd.



**KEYWORDS:** Holocene palaeoclimate; water table; transfer function; peatlands; testate amoebae.

## Introduction

A range of palaeoenvironmental evidence is available in peat deposits, including microfossils and other biological remains, physical properties and geochemical characteristics (Charman, 2002). The reconstruction of palaeohydrological conditions on ombrotrophic peatlands is of particular interest because such reconstructions can be interpreted as palaeoclimate records of water balance (Barber, 1981). Several methods have been used to reconstruct palaeohydrology, including plant macrofossils indicating changes in plant communities, and humification, a measure of relative decay. Over the last decade, testate

amoebae (a group of protists) have become established as an additional palaeohydrological indicator, especially with the advent of quantitative reconstructions from transfer functions from sites in various parts of North America, Europe and New Zealand (Warner and Charman, 1994; Charman, 1997; Woodland *et al.*, 1998; Charman and Hendon, 2000; Mitchell *et al.*, 2001; Booth and Jackson, 2003).

These studies established the relationship between testate amoebae and hydrology (measured as depth to water table) through multivariate ordination analyses. They then use training sets of modern testate amoebae assemblages and depth to water table for reconstructing hydrological changes from fossil assemblage data. To date, such reconstructions have only been carried out using modern data from a relatively limited geographical area applied to sites within the same region. Local modern training sets from the specific site or region in which the fossil data are taken may often be adequate for reconstructing past changes. However, there are a number of problems with this approach including: (1) poor or no modern analogues for some taxa; (2) difficulty in comparing results from different regions when the reconstructions are based on different transfer functions. Poor analogues often arise because the variability in the fossil record from a site is often much greater than the variability in the modern fauna from the same site and others in the local area. For example, in Britain, many fossil studies report

\*Correspondence to: D. J. Charman, School of Geography, University of Plymouth, Plymouth, Devon PL4 8AA, UK.  
E-mail: dcharman@plymouth.ac.uk

†ACCROTELM (Abrupt Climate Change Over the European Land Mass, www.glos.ac.uk/accrotelm, European Union Framework V contract number EVK2-CT-2002-00166). Project members: Jukka Alm, Sue Bartlett, Carole Begeot, Maarten Blaauw, Antony Blundell, Frank Chambers, Dan Charman, John Daniell, Richard Evershed, John Hunt, Edgar Karofeld, Atte Korhola, Hansjörg Kuester, Jukka Laine, Michel Magny, Dmitri Mauquoy, Erin McClymont, Fraser Mitchell, Pirita Oksanen, Richard Pancost, Kaarina Sarmaja-Korjonen, Heiki Seppä, Ülle Sillasoo, Bettina Stefanini, Mareike Steffens, Eeva-Stiina Tuittila, Minna Väliranta, Johannes van der Plicht, Bas van Geel, Dan Yeloff.

high abundance of taxa such as *Hyalosphenia subflava*, which occurs less frequently and in lower abundance in modern data. A more significant problem is the lack of any modern analogues for some taxa. One taxon, *Diffugia pulex* type, is the dominant in some sections of the fossil record from Britain (Hendon *et al.*, 2001; Langdon *et al.*, 2003; Blundell and Barber, 2005; Langdon and Barber, 2005), yet is not present in the modern training set used to infer past water table variability (Woodland *et al.*, 1998).

Occasionally, transfer functions have been applied to sites outside the region in which they were developed on the basis that testate amoebae have a cosmopolitan distribution and show similar responses to hydrology in different parts of the world (Charman *et al.*, 2004; Caseldine and Gearey, 2005). Again, this may produce satisfactory results, but it is much more likely to give rise to poor analogues or analogues which do not represent correct relationships between hydrology and assemblage composition for that particular area.

In this paper we tackle some of these problems by collecting and analysing new data from sites distributed over a much wider region, representing a more complete range of raised mires in Europe. A new transfer function is developed which overcomes the uncertainties inherent in applying regionally specific transfer functions, and many of the problems of no or poor analogues that were previously encountered in the transfer function for Britain. The model is tested both by cross-validation and by comparisons with the regional transfer function from Britain.

## Methods

Eight sites from across Europe were sampled for modern assemblages of testate amoebae (Fig. 1, Table 1). The sites were selected to represent the major axes of longitudinal and latitudinal variability in the raised mires of Europe. In particular, the gradient from hyperoceanic raised mires (Ireland) to continental raised mires (Estonia) was an important component of site selection. At each site, a series of three transects was established. Six sample locations along each transect were selected

to cover the microtopographical gradient from hummock to hollow, and the three transects were placed to represent any significant variation in larger-scale vegetation variability.

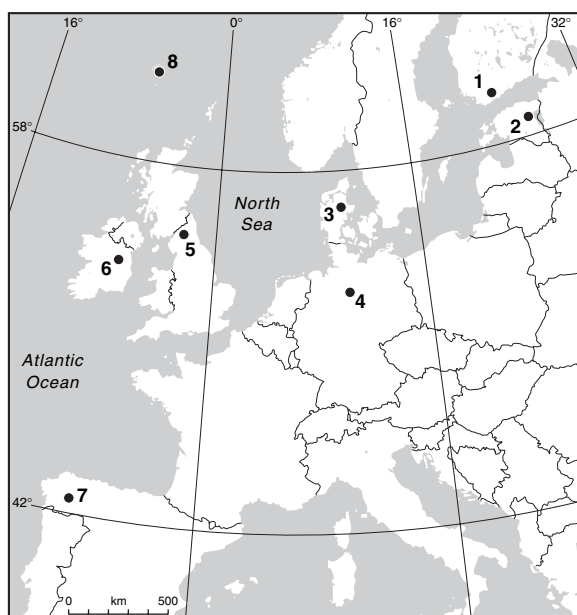
At each location, a sample of 10 × 10 cm horizontal dimensions and 5 cm depth was removed with a large serrated knife. The sample was divided into two equal halves. One half was used for analysis of testate amoebae and the other for physical peat properties (see below). At each sample location, the depth to water table, dominant plant cover in the sample and surrounding 1 m<sup>2</sup> were recorded at the time of sampling. The water table depths therefore only represent the time of sampling in the late summer of 2003. In addition, at several sites, the pH and conductivity were also measured, mainly to check the sites were all low-pH, avoiding the influence of confounding variables in the hydrological relationships investigated.

Samples were returned to the laboratory immediately after fieldwork. One half of each sample was weighed, oven-dried and reweighed to measure moisture content and bulk density. The other half of the sample was processed for testate amoebae analysis using standard techniques (Hendon and Charman, 1997), except that safranin stain was not used and samples were mostly counted in water rather than glycerol as this provides better visibility of some features. Counts were all in excess of 150 tests and identifications were made using the criteria in Charman *et al.* (2000).

The relationships between testate amoebae assemblages and hydrological variables were explored using CANOCO 4.02 (Ter Braak, 1988). Detrended correspondence analysis (DCA) on the whole raw data set was used, and taxa with low abundances or a small number of occurrences were not excluded. Canonical correspondence analysis (CCA) was used to explore the relationships between taxon assemblages and hydrological variables only as the water chemistry dataset was incomplete. C<sup>2</sup> (Juggins, 2003) was used to develop transfer functions for depth to water table and moisture content. Again, the raw percentage data were used for this and no taxa were excluded from analyses. The performance of a series of models was tested to assess which would be most suitable for reconstructing palaeohydrology for fossil assemblages, using leave-one-out cross-validation ('jack-knifing'). All RMSEP and *r*<sup>2</sup> values refer to cross-validated estimates. An optimal transfer function was further tested by comparisons with an independent modern data set from the United Kingdom (Woodland *et al.*, 1998).

## Results and discussion

There were 143 samples with counts of 150 ± 5 tests. The numbers of tests in four samples (from the Faroe Islands, Denmark and Ireland (two samples)) provided totals too low to include in further analyses. During field sampling it was not possible to measure the depth to water table at the Spanish site, because the water was too far below the surface. The Spanish data were therefore excluded from analyses that required water table data (see below). The pH and conductivity measurements confirmed that most of the sites are oligotrophic and the assemblages are therefore unlikely to be affected by differences in base and nutrient status (Table 1). The pH and conductivity values for the Faroese site are sufficiently high (pH 6.6–7.0, conductivity 53–105 µS cm<sup>-1</sup>) for the testate amoebae fauna to be influenced partly by geochemistry. Usually this influence is subordinate to that of hydrology (Tolonen *et al.*, 1994), but nevertheless it is important to be aware of this as a possibility in interpreting relationships with hydrological variables. All other sites were more typical raised mires in terms of



**Figure 1** Location of study sites. See Table 1 for further site details

**Table 1** Details of sites sampled

Number on Fig. 1	Name and country	Latitude	Longitude	Altitude (m)	Samples (n)	Water table (cm)	Moisture (%)
1	Kontolanrahka, Finland	60° 47' N	22° 47' E	87	24	0–34	80.9–97.0
2	Männikjärve, Estonia	58° 52' N	26° 14' E	82	18	0–47	87.1–95.9
3	Lille Vildmose, Denmark	56° 50' N	10° 15' E	7	18	1–31	58.8–97.1
4	Bissendorfer Moor, Germany	52° 31' N	09° 40' E	52	18	0–56	62.3–96.3
5	Butterburn Flow, England	55° 05' N	02° 30' W	280	18	5–38	77.0–96.1
6	Ballyduff bog, Ireland	53° 05' N	08° 00' W	60	18	–3–25	79.1–97.5
7	Pedrido, Spain	43° 27' N	07° 32' W	824	15	ND	75.4–93.4
8	Másaklettur, Faroe Islands	62° 10' N	06° 54' W	250	18	0–40	78.6–94.7

vegetation, with pH in the range 3.8–4.3, conductivity  $26\text{--}78\ \mu\text{S cm}^{-1}$  where it was measured. There is some suggestion of higher pH and conductivity in the more oceanic sites (pH 4.0–4.3 conductivity  $43\text{--}78\ \mu\text{S cm}^{-1}$  for England, and pH 3.8–4.0 and  $26\text{--}49\ \mu\text{S cm}^{-1}$  for Estonia).

### Testate amoebae assemblages and environmental variables

Detrended correspondence analysis (DCA) of the complete dataset shows considerable overlap in the assemblages from the different sites, confirming the cosmopolitan distribution of many taxa (Fig. 2). Bissendorfer Moor (Germany) occupies a distinctive position in the ordination space and lacks any significant overlap with the other sites. This is probably due to the high abundance of *Hyalosphenia subflava* which does not generally occur in such high levels in the other sites. Samples from this site also contain *Arcella discoides* type, an unexpected result as in studies of modern faunas, *H. subflava* is normally reported as being a very dry indicator and *A. discoides* type is usually found in wet hollows and bog pools (Corbett, 1973; Tolonen, 1986). However, these two taxa seem to have coexisted in the past, as they have been found in fossil samples (Hendon *et al.*, 2001; Blundell and Barber, 2005). Some of the Spanish and Faroese samples are also positioned closer to the German samples, suggesting that there are some similarities in the fauna from these sites. The species ordination mostly appears to reflect a hydrological gradient from wet (low values) to dry (high values) along axis 1 (Fig. 2(b)). The main exception to this is *A. discoides* type and its anomalous association with relatively dry taxa. The relationship between taxa and hydrological status is discussed in greater detail below.

Constrained ordination analysis using canonical correspondence analysis (CCA) was carried out on the dataset, excluding the Spanish samples where water table data were unavailable (Fig. 3). The main axis of variation is clearly related to hydrological status with percentage moisture and depth to water table occurring at opposite ends of axis 1. A Monte Carlo permutation test shows this axis is significant ( $p < 0.001$ ). Further tests on the moisture and water table variables on their own show they are both significant at  $p < 0.001$ . Both variables explain 7.0% of the total taxon variability on their own, or 13.4% together. Bulk density is a secondary gradient and separates many of the samples from Bissendorfer Moor (Germany) from the others. Bulk density explains 5.3% of the variability on its own and 16.8% when combined with the other two variables. Despite the higher pH of the Faroe Islands site, the samples do not form an outlying group suggesting the influence of base status is insignificant for these samples.

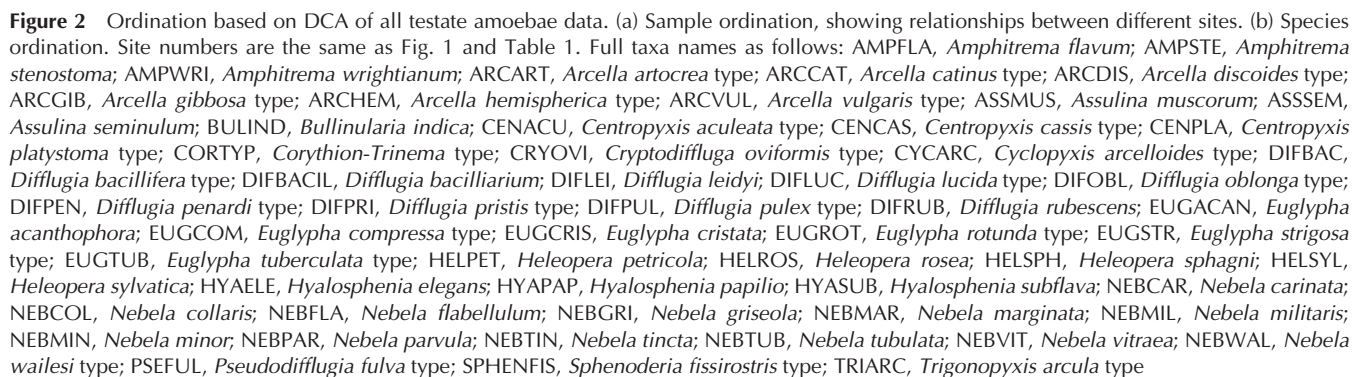
A plot of taxon distribution over the main hydrological gradients shows that many taxa show a strong relationship with

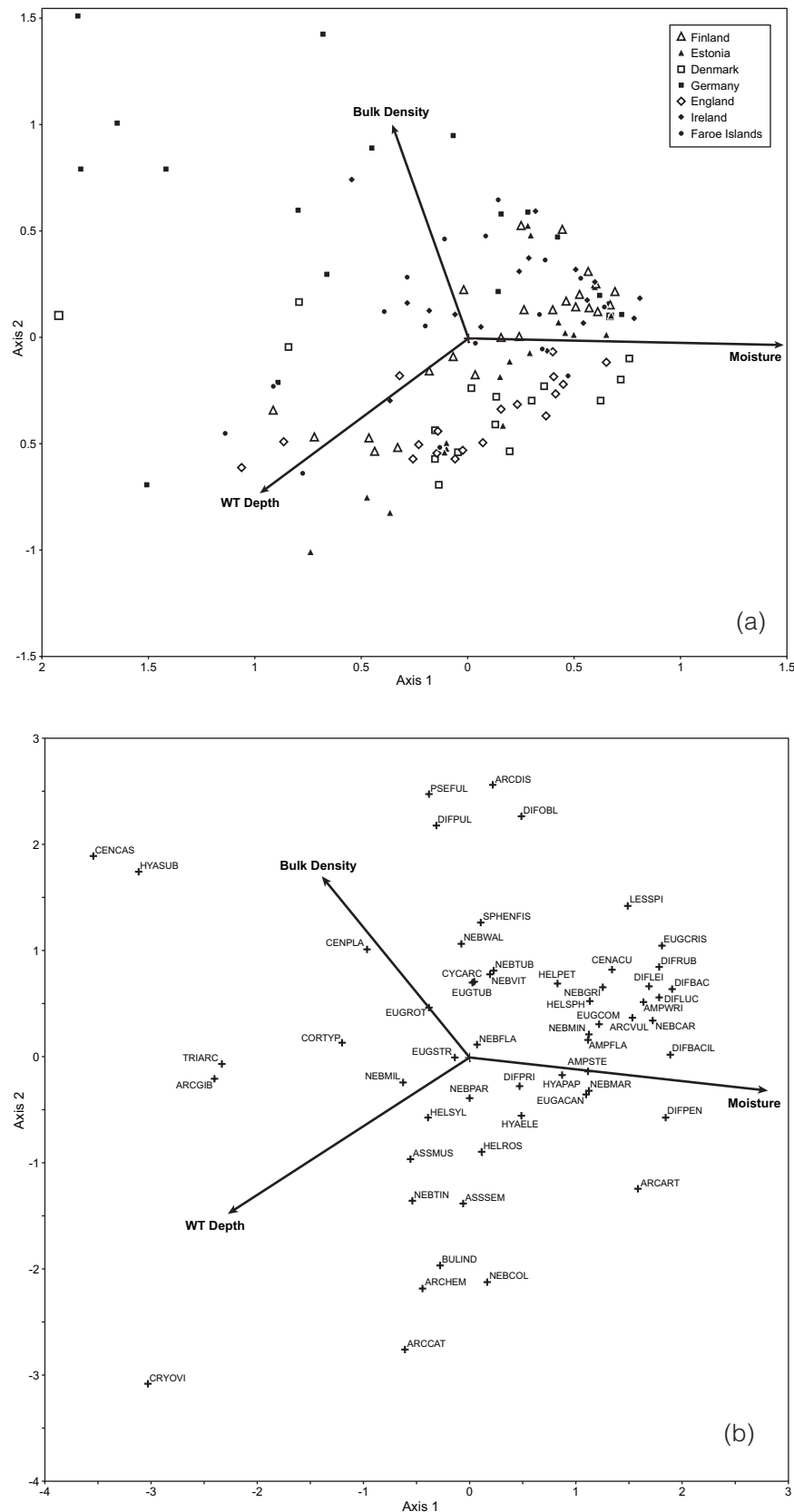
both depth to water table and moisture content (Fig. 4). Taxa at the wet end of these gradients are more likely to be restricted to a narrow range of conditions than those at the drier end of the gradients. Wet-indicating taxa rarely occur in relatively dry locations but dry-indicating taxa are often present in low amounts in relatively wet locations. The implications of this finding are discussed below.

### Transfer function development

The testate amoebae data show strong relationships with both moisture and depth to water table. This is not surprising as the two variables are correlated with each other ( $r = 0.53$ ,  $p < 0.001$ ). The moisture content shows much more variability than the water table and there is a subgroup of samples where the moisture content is much lower than would be expected from the position of the water table (Fig. 5). Almost all of these outlier samples are from Bissendorfer Moor, Germany, confirming that there is something unusual about many of these samples. These samples also had a generally higher bulk density than those from other sites, which would tend to produce lower moisture content by weight. The reasons for these unusual physical characteristics are unknown, but drainage or fire are both possible causes. Although there is no evidence on the surface for either of these having influenced the sample locations, it is possible that the vegetation has recovered sufficiently to mask the effects of earlier damage. It is likely that moisture content is a less reliable parameter than depth to water table, owing to much greater short-term (diurnal and day-to-day) variability in the field and the potential for evaporative loss during and after sampling. The transfer function development and testing therefore focused principally on water table, although moisture data were also analysed for comparison.

The performance of several different models for water table was very similar, with a two-component weighted average partial least squares (WAPLS) model the best-performing model (RMSEP = 7.64 cm,  $r^2 = 0.60$ ) (Table 2). The tolerance down-weighted weighted average model (WA-Tol) displayed very similar performance and other less conventionally used models such as a weighted average modern analogue technique (WMAT) also produced similar statistics. Comparisons of the observed and predicted water tables from the analysis showed that the performance of the model was particularly poor for a few samples with very deep water tables (Fig. 6(a)). These were removed following screening of the samples with residuals greater than 20% of the full range (11.8 cm). These samples may have been affected by problems of non-equilibration of water tables before measurement. A model based on the removal of the screened samples resulted in an improved RMSEP of 5.6 cm with an  $r^2$  of 0.71 for the WAPLS two-component model and a marked improvement in the WMAT model



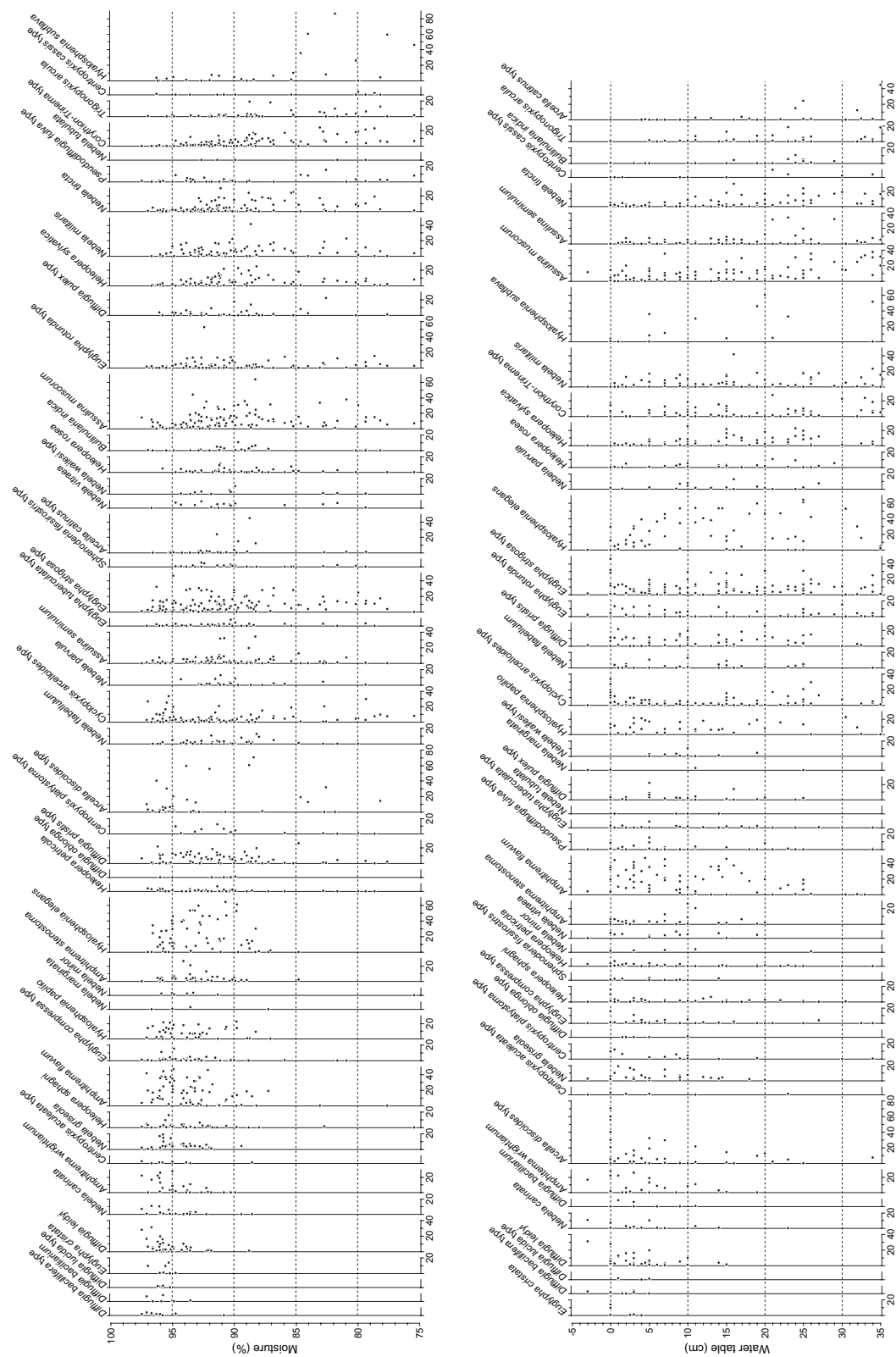


**Figure 3** Constrained ordination from CCA of all samples excluding the Spanish data where water table data were unavailable. (a) Sample ordination grouped by site. (b) Species–environment biplot. Numbers are the same as Fig. 1 and Table 1. Taxa abbreviations as in Fig. 2

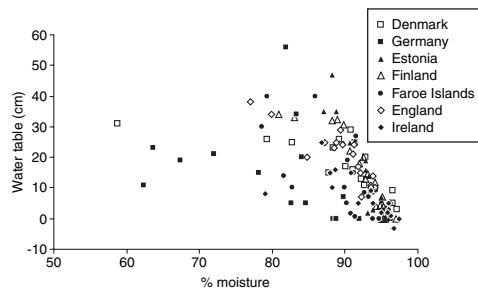
(RMSEP = 5.6 cm,  $r^2 = 0.74$ ). Given the sensitivity of the WMAT model to outlying samples the WAPLS model is probably more reliable and this remains our favoured model (Fig. 6(b)), despite the marginally higher  $r^2$  for WMAT. Interestingly, the screened samples were not predominantly from the German site that appeared to have a rather different assem-

blage composition from most other sites in the ordination analyses. To provide a further check on whether the German samples are anomalous in terms of their relationship with water table, the WAPLS 2 component model was run with the German samples outside the training set. The predicted water tables for the German samples were strongly correlated with





**Figure 4** Distribution of taxa (percentage abundance) with  $n > 4$  plotted against water table and moisture content. Taxa are arranged in order of their optima on the gradients as determined from the transfer functions. Zero values are not shown—the values close to the y-axis are very low percentage values. See text for details



**Figure 5** Relationship between percentage moisture and water table depth for all samples, categorised by site. Site symbols as in Figs 2 and 3

their observed values ( $r^2 = 0.74$ ). This implies that despite the unusual properties of the German samples, their inclusion in the transfer function has not had a distorting influence on the inferred water table values.

A transfer function for moisture was also tested (Table 3). Surprisingly, the performance of both modern analogue techniques (MAT) was significantly better than the other approaches which are more conventionally used. The WMAT results yielded an RMSEP of 4.46% and an  $r^2$  of 0.58. Although there were concerns over the quality of some aspects of the moisture data, these results are similar to those for water table. Again, screening resulted in significant improvement to the performance of the WMAT model (RMSEP = 2.67%,  $r^2 = 0.71$ ) and suggests that the reconstruction of moisture levels is also possible using this dataset. In screening, most of the samples removed were also extreme dry samples. These are likely to underestimate average moisture levels because of greater

short-term variability in moisture content and perhaps due to the effects of sample transport and storage. However, the performance of the model is still poor for drier samples, and most of the inferred values are highly overestimated at this end of the gradient (Fig. 7). The good performance of the MAT models for both moisture and water table transfer functions is a surprising finding, although these models have not been extensively tested in testate amoebae studies. However, given the potential problems of autocorrelation in MAT approaches, the weighted average based techniques may provide more robust reconstructions (Telford and Birks, 2005). Although we would expect this effect to be less marked for samples from ombrotrophic peatlands, spatial autocorrelation might be expected between samples from the same sites, which could affect the accuracy of reconstructions.

### Hydrological optima for taxa

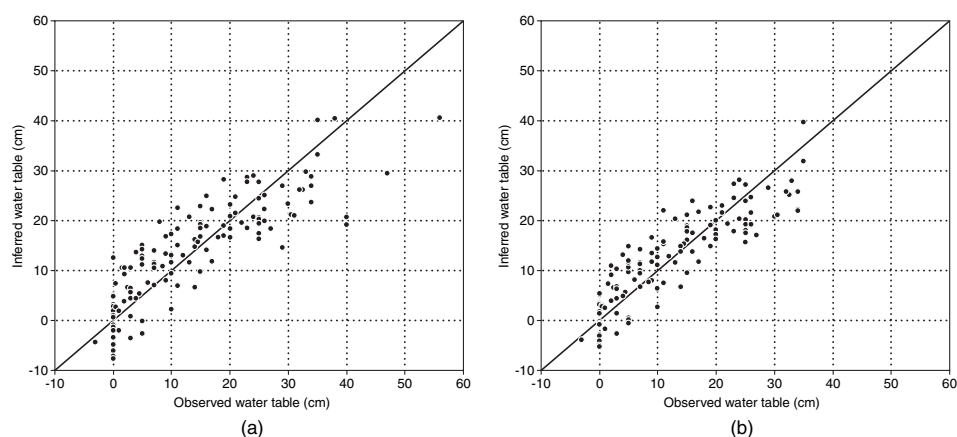
Taxon optima show a typical pattern for both water table and moisture (Fig. 8). The general order of taxa is similar to many other studies (see Charman *et al.* (2000) for a review), with taxa such as *Diffugia bacillifera*, *D. bacillarium*, *Nebela carinata* and *Amphitrema wrightianum* at the wettest end of the gradient and *Hyalosphenia subflava*, *Trigonopyxis arcuata*, *Bullinularia indica* and *Corythion-Trinema* type at the driest end of the gradient.

There are some differences in the relative positions of some taxa on the water table and moisture gradients (Fig. 8). To compare the relative positions on the gradients, the rank position on

**Table 2** Summary of performance of different models for water table using the full dataset, based on jack-knifed ('leave-one-out') cross-validation and in order of performance assessed by the root mean squared error of prediction (RMSEP). Only the 'best' version of each main approach is shown. Figures in parentheses are following exclusion of outlier samples identified from the WAPLS analysis

Model	$R^2$	Average bias	Max. bias	RMSEP
WAPLS Component 2	0.60 (0.71)	0.31 (0.05)	26.6 (8.5)	7.64 (5.63)
WA-Tol (inverse deshrinking)	0.60 (0.67)	0.56 (0.27)	30.6 (9.5)	7.65 (5.97)
PLS Component 4	0.59 (0.68)	0.23 (0.02)	26.1 (8.2)	7.78 (5.86)
WMAT	0.59 (0.74)	-0.48 (-0.40)	37.5 (9.6)	7.90 (5.60)
WA (inverse deshrinking)	0.55 (0.66)	0.30(0.09)	30.8 (6.8)	8.13 (6.88)

Abbreviations: WA, weighted average; WA-Tol, weighted average (tolerance downweighted); WAPLS, weighted averaging partial least squares; WMAT, modern analogue technique (weighted average of 10 closest analogues); PLS, partial least squares.



**Figure 6** Predicted and observed water tables from the two-component WAPLS model (a) on the entire dataset, (b) after screening to remove data with high residuals



**Table 3** Summary of performance of different models for moisture using the full dataset, based on jack-knifed ('leave-one-out') cross-validation and in order of performance assessed by the root mean squared error of prediction (RMSEP). Only the 'best' version of each main approach is shown. Figures in parentheses are following exclusion of outlier samples identified from the MAT analysis

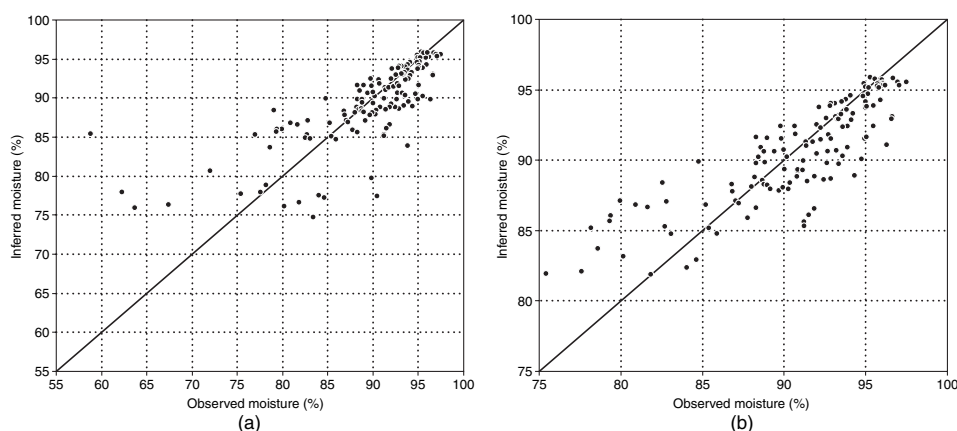
Model	$R^2$	Average bias	Max. bias	RMSEP
WMAT	0.58 (0.71)	0.28 (0.25)	21.1 (6.3)	4.46 (2.26)
WA-Tol (inverse deshrinking)	0.50 (0.62)	-0.17 (-0.05)	24.0 (7.9)	4.87 (2.97)
PLS Component 4 (component 5)	0.50 (0.65)	-0.05 (0.02)	25.2 (6.7)	4.91 (2.91)
WAPLS Component 1 (component 3)	0.48 (0.64)	-0.11 (0.05)	23.0 (5.8)	4.98 (2.95)
WA (inverse deshrinking)	0.48 (0.57)	-0.11 (-0.01)	23.0 (8.8)	4.98 (3.12)

Abbreviations: WA, weighted average; WA-Tol, weighted average (tolerance downweighted); WAPLS, weighted averaging partial least squares; WMAT, modern analogue technique (weighted average of 10 closest analogues); PLS, partial least squares.

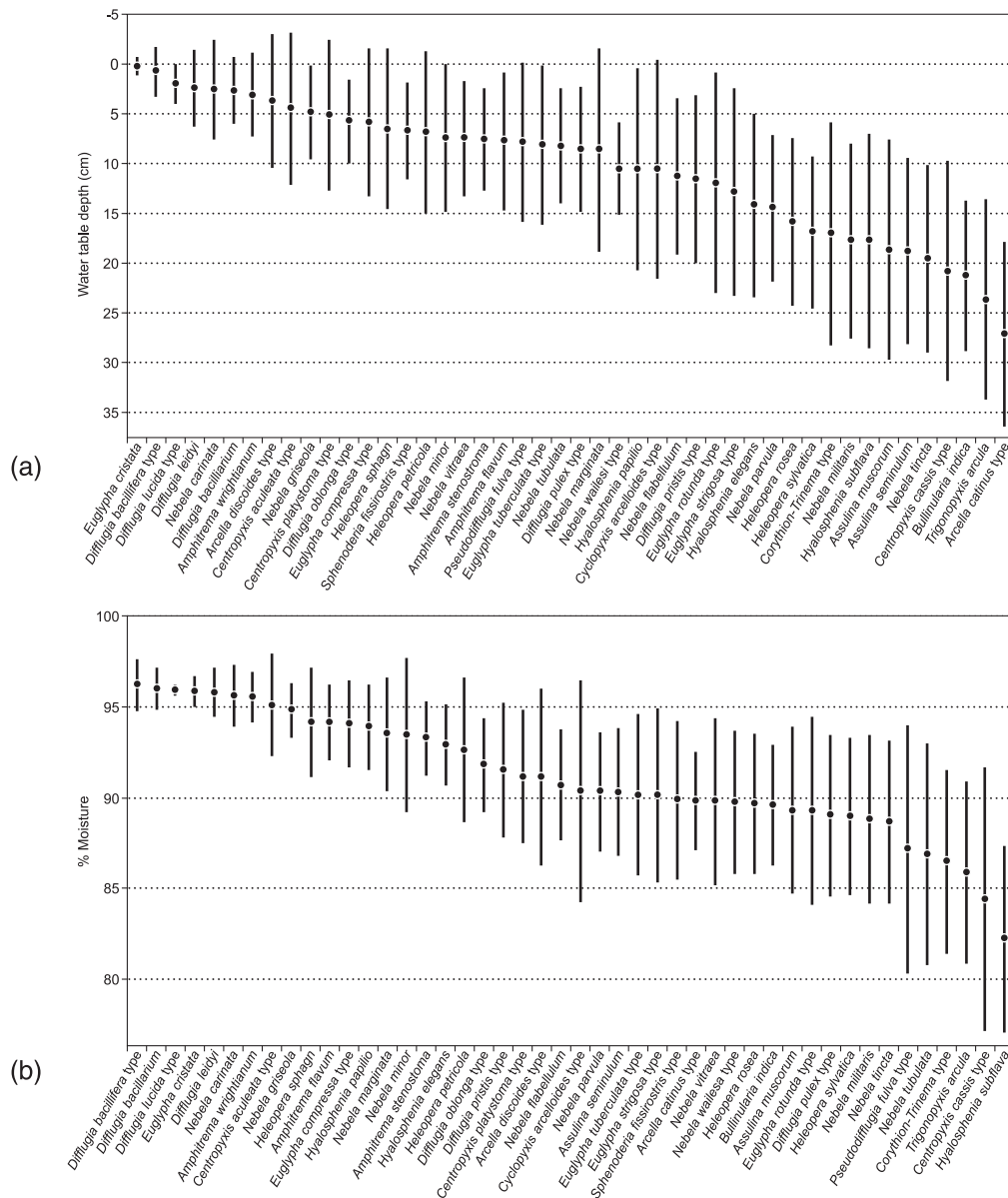
each gradient was calculated for all 46 taxa occurring in >3 samples. The difference in ranking was expressed as the water table rank minus the moisture rank (Fig. 9). While many taxa occur in similar positions on the gradients, there are two clear groups of taxa which tend to occur in relatively wet or relatively dry positions on the water table gradient compared to their position on the moisture gradient. Some of these taxa have low frequency and therefore estimates of optima are subject to greater error. Notable taxa which are more than 10 rank points wetter in the water table gradient and occur in a large number of samples (>20) are *Pseudodifflugia fulva* type, *Arcella discoides* type and *Difflugia pulex* type. Using similar criteria, the taxa that are in locations at the drier end of the water table gradient are *Hyalosphenia papilio*, *Assulina seminulum* type, *Arcella catinus* type and *H. elegans*. Some of the rank differences illustrated in Fig. 9 may arise from differences in the training sets used for moisture and water table transfer functions and the fact that a number of samples with intermediate water tables have lower than expected moisture content (Fig. 5). However, a repeat analysis for moisture using exactly the same subset of data that was used for water table ( $n = 119$ ) highlighted the same subset of taxa, implying that there are fundamental differences between taxa and their relationship with the different hydrological parameters. Some taxa appear to require a higher water table but are able to survive relatively lower moisture content (*Pseudodifflugia fulva* type, *Arcella discoides* type, *Difflugia pulex* type). Other taxa require relatively high moisture content even though they tend to occur where water tables are relatively low (*Hyalosphenia papilio*, *Assulina seminulum* type, *Arcella catinus* type, *H. elegans*). However, a further consideration is the fact that the ranking is not linear with each rank representing a larger increment in some parts

of the gradient, especially towards the dry end. For example although *Hyalosphenia papilio* is ranked 14 places higher on the moisture gradient than on the water table gradient, it is still within 'mid-range' values on both. In applying transfer functions, it may be valuable to reconstruct both water table and moisture for fossil sequences, to try to differentiate between these two variables for past hydrological changes. However, it seems unlikely that there will be large differences between reconstructed water tables and reconstructed moisture levels, unless assemblages are dominated by the taxa identified above. *Difflugia pulex* type is perhaps the most abundant of these taxa in fossil sequences. Its abundance in mid-Holocene sequences may suggest conditions with higher water table but low moisture content, perhaps related to more intense desiccation by wind and/or insolation.

Besides the optimum values for individual taxa, it is clear that the tolerances and ranges also vary along the hydrological gradients. In particular, the calculated tolerances (Fig. 8) and the full ranges (Fig. 4) of taxa with wet optima have much more restricted distributions than those with dry optima. Thus reconstructions during phases of wetter conditions are likely to be more accurate and precise than those for dry phases. For dry conditions, the lack of wet and intermediate indicators is perhaps a better indicator of hydrology than the presence of dry taxa. Low abundances of dry indicators in wetter sites may be a result of greater tolerance of wet conditions by the taxa concerned, or perhaps more likely because of the occurrence of a limited number of dry microscopic niches within the surface moss layers in otherwise generally wet locations. These small microsites would allow small numbers of xeric amoebae to coexist with more hygrophilous taxa, but would limit their abundance.



**Figure 7** Predicted and observed moisture content from the modern analogue technique using the weighted average of the 10 nearest analogues (a) on the entire dataset, (b) after screening to remove data with high residuals



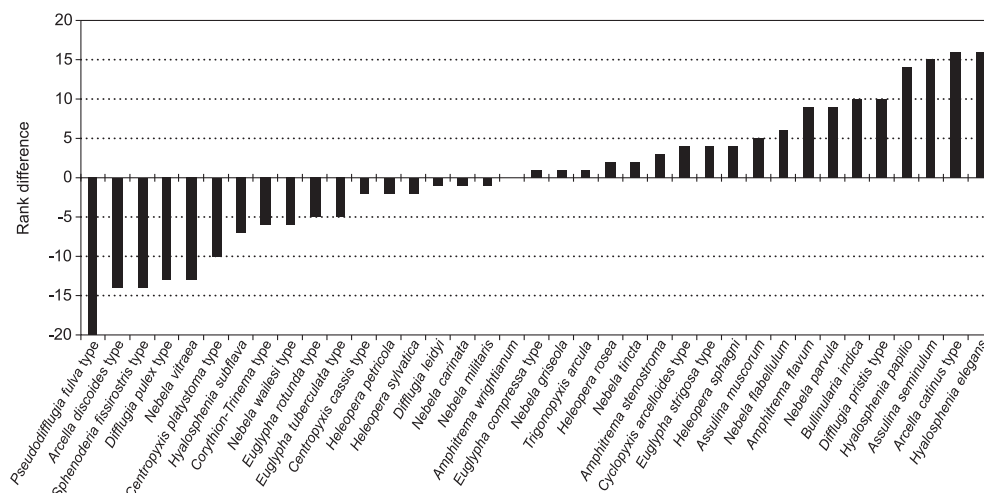
**Figure 8** Optima and tolerances from the screened data sets based on weighted averaging for (a) depth to water table ( $n = 119$ ), and (b) moisture ( $n = 132$ )

## Improving analogues

A notable taxon in the transfer function is *Diffugia pulex* type, which has occurred frequently and in abundance in fossil datasets from Britain and elsewhere, but does not appear in the British training set of Woodland *et al.* (1998) and therefore has no good modern analogue data. This taxon appears at intermediate (water table) and slightly drier (moisture) positions in the hydrological gradient in the European data. The data are good quality with 36 samples in the moisture training set and 26 in the water table training with a maximum abundance of 23% of the total fauna (Fig. 10). These results support the hypothesis that *D. pulex* is a taxon of moderately dry conditions as suggested by Hendon (1998). *D. pulex* type is also one of the taxa that occurs in wetter locations on the water table gradient than it does on the moisture gradient (see above). It occurs most frequently in the Spanish, Irish and Faroese samples and is absent (except for a single occurrence) in the Estonian and Finnish samples, suggesting that it is a taxon mainly of oceanic conditions. It was also found in fewer samples and generally low abundance in the British, German and Danish samples, although the highest single abundance was recorded in one of the German samples with low moisture content.

Other taxa for which the analogues are very much improved are several of the drier indicators. In particular, *Hyalosphenia subflava* is a taxon for which modern European data are sparse, particularly in the UK training set, although reasonably good for some North American studies (Charman, 1992; Warner and Charman, 1994; Booth, 2002). In the European dataset there are 26 occurrences at up to 87% abundance in the moisture data set and 19 occurrences at up to 61% in the water table training set (Fig. 10). All the samples with high abundances of *H. subflava* were from either Spain or Germany. Both these sites had generally low moisture levels in the surface and water tables were low. The new data confirm this taxon as being one of the driest indicators on oligotrophic peatlands and provide much better modern analogues for samples dominated by *H. subflava*. Despite the improvements to estimates of optima and tolerances for *H. subflava* and *D. pulex* type it is still desirable to obtain further data from a wider range of locations within Europe to refine the hydrological niche estimates, and especially to have more analogues with very high abundances.

Finally, several taxa for which no data or only occasional records previously existed are also recorded here, including *Euglypha cristata*, *Nebela wailesi* type, and *Sphenoderia fissiro-*



**Figure 9** Differences in the relative ranking of taxa along the moisture and water table gradients. Taxa with  $n < 10$  are excluded. The rank difference is expressed as the water table ranking minus the moisture ranking. Taxa to the left are placed in wet positions and taxa to the right are in dry positions on the water table gradient relative to the moisture gradient

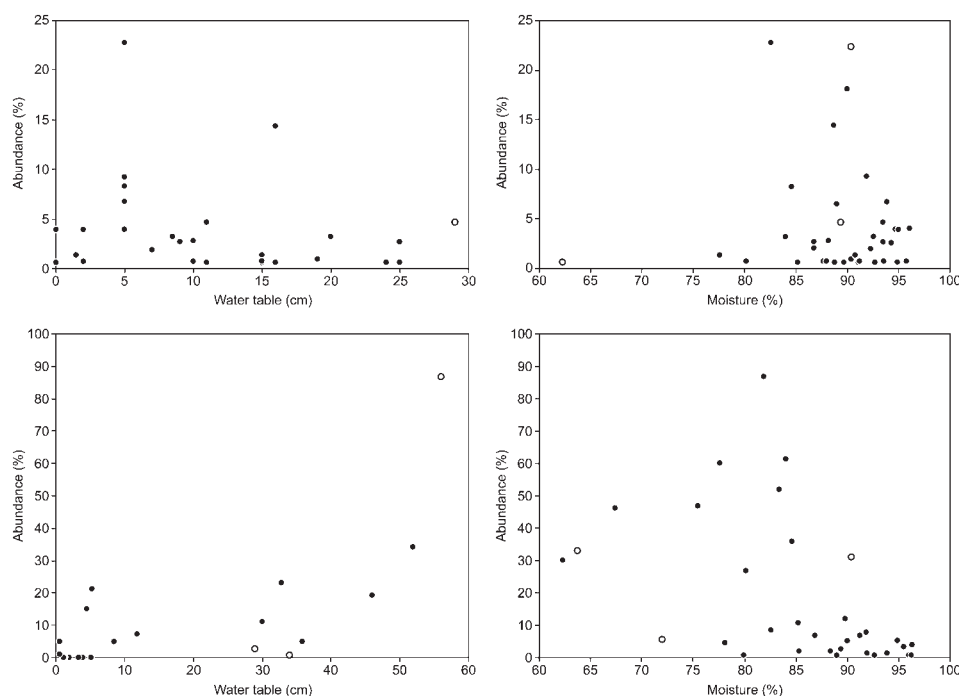
*ostris* type, but it is not yet clear how common these taxa are in fossil sequences from European sites. Several of these taxa are also present only in low abundance in a small number of modern samples so that optima and tolerances are less certain than for other better known taxa.

### Testing the transfer function

A further test of the transfer function was undertaken by using an independently derived data set from the British training set (Woodland *et al.*, 1998), which has been extensively applied to data from the United Kingdom and sometimes to data elsewhere in Europe (Charman *et al.*, 2004, 2006). These data con-

sist of 160 samples from sites where long-term water table monitoring data were available; hence the mean annual values are more reliable than the single measurements taken in most studies. If the model is performing in the same way on unknown data, the mean prediction errors (as compared to observed values) should be similar to those found in cross-validation. In this case, the mean prediction error was 5.4 cm, very similar to the RMSEP of 5.6 cm obtained from cross-validation. The predictions were also generally for drier conditions than observed, with the mean residual being 1.8 cm deeper than the observed values.

The British transfer function was also applied to the European data and yielded much poorer results. The mean error in predictions for the European dataset was 9.4 cm, compared with an RMSEP of 4.0 cm for jack-knifed cross-validation of



**Figure 10** Abundance of *Diffugia pulex* type (top) and *Hyalosphenia subflava* (bottom) against water table depth and moisture content. Open circles show samples which were identified as outliers in the transfer functions, using the overall relationship between taxa assemblages and the hydrological variable of interest

the British data. In addition, the predictions from the British data were almost all too low by an average of 8.5 cm, with much wetter conditions predicted than actually observed.

The results can be explained in two main ways. First, the range of variability sampled in the European data is much wider than that for the British transfer function. The performance of the European transfer function is good when applied to the British data, but the British data are poor at inferring values for peatlands from a wider region. This suggests that despite the cosmopolitanism of testate amoebae, the assemblages of these taxa vary considerably across the continent. This is also suggested by the ordination analyses where some sample sites occupy different parts of the ordination space. Data from North America support the idea that assemblages vary at the sub-continental scale, although many individual taxa are cosmopolitan. The hydrological indicator value of taxa is similar over broad regions, but the detail of community composition differs (Charman and Warner, 1997; Booth and Zygmunt, 2005). Second, the British data are annual average data, which are likely to be generally lower than the early summer and autumn water tables sampled in the European dataset, partly explaining the differences in average residual values.

### Applying the transfer function to fossil data

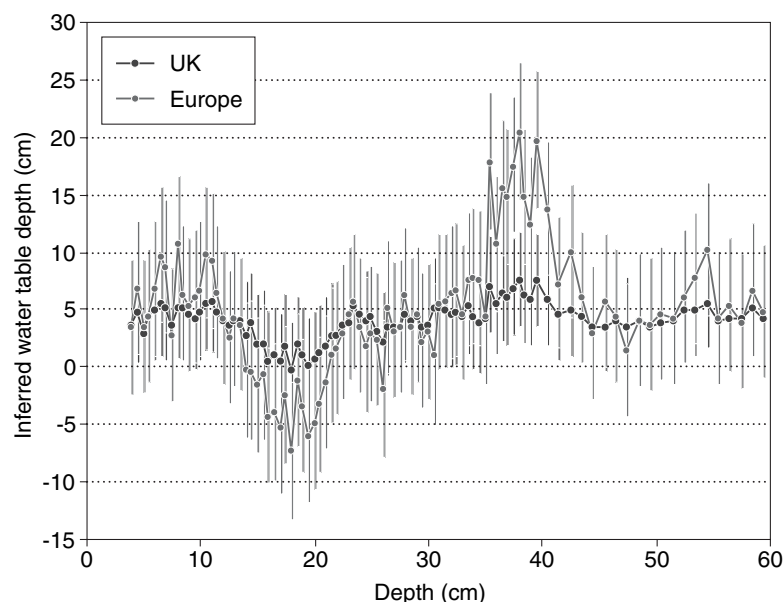
As a final test of the comparability of the transfer function with the existing UK transfer function, reconstructions of a high-resolution core from Butterburn Flow, England, were carried out. The data are those presented by (Hendon and Charman, 2004) and document water table changes on a raised mire in northern England over the past 300–400 yr, although only the dating for the last 200 years is secure. A reconstruction was made using the WAPLS 2 component water table transfer function and this was compared with the original reconstruction based on the British transfer function (Fig. 11). The linear correlation between the two reconstructions is 0.94 with an  $r^2$  of 0.88. It is clear that the overall patterns of change are very similar but that the magnitude of change inferred from the European transfer function is much greater than that of the British transfer

function. The same reasons discussed above explain some of the differences in the reconstructions, but the use of mean annual average data in the British transfer function does not produce systematically wetter values for all samples. While there is an overall bias to wetter values in the British reconstruction of about 0.8 cm, both the dry and wet periods are greater in magnitude in the European reconstruction. Presumably this is due to the greater range of sampled variation which 'stretches' the relative wetness gradient. This influence overrides the influence from the bias towards sampling mostly relatively wet sites in the UK training set. The prediction error estimates are also slightly higher from the European transfer function (approximately 5.5 cm compared to 4.1 cm). However, the precision of the reconstruction is higher relative to the overall range of reconstructed values and represents an improved signal-to-noise ratio. It is also interesting to note that the inclusion of the previously missing analogue taxon, *Difflogia pulex*, in the new transfer function has not resulted in significant difference in the main patterns of reconstructed changes. The fossil assemblages include up to 50% *D. pulex*, similar to many other fossil assemblages.

### CONCLUSIONS

The development of a transfer function for depth to water table from testate amoebae analysis on European ombrotrophic peatlands provides a significant improvement to existing transfer functions within the European region. It will therefore provide the basis for improved palaeoclimatic reconstructions from ombrotrophic peatland records in this region. In addition, the exploration and analysis of the data provides more general insights into the development and application for transfer functions in other parts of the world and perhaps for other groups of organisms. The extent to which these insights are applicable to other organisms will depend on their biology, ecology and, particularly, their biogeography.

- 1 The inclusion of a larger range of sites representing much of the raised mire variability in Europe has resulted in an



**Figure 11** Reconstructions of water table for a core from Butterburn Flow, England, based on the European (this paper) and UK (Woodland *et al.*, 1998) transfer functions. Error bars show estimated errors of prediction based on bootstrapping

increased range of analogues for fossil assemblages. A good example of this is the establishment of analogues for *Diffugia pulex* type and improved analogues for samples with abundant *Hyalosphenia subflava*. Despite intensive sampling in Britain, including from sites where these taxa formerly occurred in abundance, no good modern analogues had previously been found. This demonstrates the need for modern training sets which encompass a much broader range of modern conditions than currently occur within relatively small regions such as Britain. Analogues for fossil assemblages must sometimes be sought outside of the region from which the fossil records are derived. This is a classical problem in palaeoecology (Lowe and Walker, 1997), but one which becomes particularly acute in the application of quantitative transfer functions where the absence of an analogue taxon or poor quality data for a taxon can seriously limit the reliability of the inferences made. There is sometimes a tendency to accept uncritically results based on such inferences from quantitative approaches.

- 2 Tests of the European transfer function by comparison with an independent modern dataset from Britain suggest that hydrological variability for a smaller region can be inferred accurately from the European data. In contrast, the transfer function from Britain cannot be applied reliably to the broader European region. This is probably because of the wider range of assemblages represented in the European data. This finding is surprising given the cosmopolitanism of testate amoebae. It is well known that the same taxa occur over very large areas of the world (Tolonen, 1986), and most of the same taxa occur in almost all North American and European studies on ombrotrophic peatlands. Despite the overall cosmopolitanism of testate amoebae, their assemblages clearly vary over smaller geographical scales.
- 3 The European transfer function produces similar results to the British transfer function for recent fossil faunas for a site in England. Directional changes are the same but the magnitude of inferred change is greater from the European transfer function. This suggests that both are relatively robust for quantifying relative changes but there is greater uncertainty over the absolute values of reconstructed changes. This is partly affected by the sampling range in the modern data and highlights the need for samples to be taken across a broad range of the environmental gradient of interest and for samples to be as evenly distributed along this gradient as possible.

**Acknowledgements** The ACCROTELM project is funded by the European Union Framework V under contract number EVK2-CT-2002-00166. We wish to thank Pete Langdon and Bob Booth for refereeing this paper and improving the final version.

## References

- Barber KE. 1981. *Peat Stratigraphy and Climatic Change*. Balkema: Rotterdam.
- Blundell A, Barber K. 2005. A 2800-year palaeoclimatic record from Tore Hill Moss, Strathspey, Scotland: the need for a multi-proxy approach to peat-based climate reconstructions. *Quaternary Science Reviews* **24**: 1261–1277.
- Booth RK. 2002. Testate amoebae as paleoindicators of surface-moisture changes on Michigan peatlands: modern ecology and hydrological calibration. *Journal of Paleolimnology* **28**: 329–348.
- Booth RK, Jackson ST. 2003. A high-resolution record of late-Holocene moisture variability from a Michigan raised bog, USA. *The Holocene* **13**: 863–876.
- Booth RK, Zygmunt JR. 2005. Biogeography and comparative ecology of testate amoebae inhabiting *Sphagnum*-dominated peatlands in the Great Lakes and Rocky Mountain regions of North America. *Diversity and Distributions* **11**: 577–590.
- Caseldine C, Gearey B. 2005. A multiproxy approach to reconstructing surface wetness changes and prehistoric bog bursts in a raised mire system at Derryville Bog, Co. Tipperary, Ireland. *The Holocene* **15**: 585–601.
- Charman DJ. 1992. Relationship between testate amoebae (Protozoa: Rhizopoda) and microenvironmental parameters on a forested peatland in northeastern Ontario. *Canadian Journal of Zoology* **70**: 2474–2482.
- Charman DJ. 1997. Modelling hydrological relationships of testate amoebae (Protozoa: Rhizopoda) on New Zealand peatlands. *Journal of the Royal Society of New Zealand* **27**: 465–483.
- Charman DJ. 2002. *Peatlands and Environmental Change*. Wiley: Chichester.
- Charman DJ, Hendon D. 2000. Long-term changes in soil water tables over the past 4500 years: relationships with climate and North Atlantic atmospheric circulation and sea surface temperature. *Climatic Change* **47**: 45–59.
- Charman DJ, Warner BG. 1997. The ecology of testate amoebae (Protozoa: Rhizopoda) in oceanic peatlands in Newfoundland, Canada: modelling hydrological relationships for palaeoenvironmental reconstruction. *Ecoscience* **4**: 555–562.
- Charman DJ, Hendon D, Woodland WA. 2000. *The Identification of Peatland Testate Amoebae*. Technical Guide, Quaternary Research Association: London.
- Charman DJ, Brown AD, Hendon D, Karofeld E. 2004. Testing the relationship between Holocene peatland palaeoclimate reconstructions and instrumental data at two European sites. *Quaternary Science Reviews* **23**: 137–143.
- Charman DJ, Blundell A, Chiverrell RC, Hendon D, Langdon PG. 2006. Compilation of non-annually resolved Holocene proxy climate records: stacked Holocene peatland palaeo-water table reconstructions from northern Britain. *Quaternary Science Reviews*, in press.
- Corbett SA. 1973. An illustrated introduction to the testate rhizopods in *Sphagnum*, with special reference to the area around Malham Tarn, Yorkshire. *Field Studies* **3**: 301–322.
- Hendon D. 1998. *Robustness and precision of Holocene palaeoclimatic records from peatlands using testate amoebae*. PhD thesis, University of Plymouth.
- Hendon D, Charman DJ. 1997. The preparation of testate amoebae (Protozoa: Rhizopoda) samples from peat. *The Holocene* **7**: 199–205.
- Hendon D, Charman DJ. 2004. High-resolution peatland water-table changes for the past 200 years: the influence of climate and implications for management. *The Holocene* **14**: 125–134.
- Hendon D, Charman DJ, Kent M. 2001. Palaeohydrological records derived from testate amoebae analysis from peatlands in northern England: within-site variability, between-site comparability and palaeoclimatic implications. *The Holocene* **11**: 127–148.
- Juggins S. 2003. *C<sup>2</sup> User guide. Software for Ecological and Palaeoecological Data Analysis and Visualisation*. University of Newcastle: Newcastle upon Tyne.
- Langdon PG, Barber KE. 2005. The climate of Scotland over the last 5000 years inferred from multiproxy peatland records: inter-site correlations and regional variability. *Journal of Quaternary Science* **20**: 549–566.
- Langdon PG, Barber KE, Hughes PDM. 2003. A 7500-year peat-based palaeoclimatic reconstruction and evidence for an 100-year cyclicity in bog surface wetness from Temple Hill Moss, Pentland Hills, south-east Scotland. *Quaternary Science Reviews* **22**: 259–274.
- Lowe JJ, Walker MJC. 1997. *Reconstructing Quaternary Environments*. Longman: Harlow.
- Mitchell EAD, van der Knaap WO, van Leeuwen JFN, Buttler A, Warner BG, Gobat JM. 2001. The palaeoecological history of the Praz-Rodet bog (Swiss Jura) based on pollen, plant macrofossils and testate amoebae (Protozoa). *The Holocene* **11**: 65–80.

- Telford RJ, Birks HJB. 2005. The secret assumption of transfer functions: problems with spatial autocorrelation in evaluating model performance. *Quaternary Science Reviews* **24**: 2173–2179.
- Ter Braak CJF. 1988. CANOCO—an extension of DECORANA to analyse species–environment relationships. *Vegetatio* **75**: 159–160.
- Tolonen K. 1986. Rhizopod analysis. In *Handbook of Holocene Palaeoecology and Palaeohydrology*, Berglund BE (ed.). Wiley: Chichester; 645–666.
- Tolonen K, Warner BG, Vasander H. 1994. Ecology of testaceans (Protozoa, Rhizopoda) in mires in southern Finland: II, Multivariate analysis. *Archiv Fur Protistenkunde* **144**: 97–112.
- Warner BG, Charman DJ. 1994. Holocene changes on a peatland in northwestern Ontario interpreted from testate amebas (Protozoa) analysis. *Boreas* **23**: 270–279.
- Woodland WA, Charman DJ, Sims PC. 1998. Quantitative estimates of water tables and soil moisture in Holocene peatlands from testate amoebae. *The Holocene* **8**: 261–273.